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STUDIES IN THE GENUS ENTORRHIZA C. WEBER

BY

C. FERDINANDSEN AND Ö. WINGE

WITH 8 FIGURES IN THE TEXT

KØBENHAVN
H. HAGERUP'S BOGHANDEL
BIANCO LUNOS BOGTRYKKERI
1914

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Studies in the genus Entorrhiza C. Weber.

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I. The spore formation in Entorrhiza digitata Lagerh.

A rich material belonging to this species was benevolently sent to us by professor G. Lagerheim in Stockholm. It was fixed in chrom-acetic acid and very well preserved so that microtome cuts, which were stained with Heidenhains hematoxyline, proved good objects for a closer study of the spore formation. The three spore forms as they are described and figured by Lagerheim were found mixed together (cfr. our figures 1, *f—n* from Danish material), viz. [1]) some very coarsely and unevenly warted, [2]) some others lower and more evenly warted, while [3]) a third form of spores were entirely smooth and very thick-walled. The shape was always exactly globular and the size varied near 18 μ in diameter, some few however reaching 30 μ or more across.

Already P. Magnus (1878) and C. Weber (l. c.) state that the spores in *Entorrhiza* are formed apically on screw-shaped »sterigmata«, and Weber figures these organs in *E. Aschersoniana*, while P. Magnus gives a picture from *E. cypericola*, a copy of which is found in our fig. 8. Using the highest power of the microscrope, however, we saw that the spores in *E. digitata* are formed not on a single »sterigma«, but as a rule by joining of two. The most common case is figured in fig. 1, a, where the two spore-forming filaments are seen like somewhat screwed strings adhering to the ripe spore. In some successful slides we happened to see that the spore no doubt is formed by the working-together of two spiral filaments twining around each other, and that the outside walls of the filaments simply are continued into the spore-

membrane so that the spore must be due to the swelling of the fusing hyphae (fig. 1, *b*—*c*). Very often, however, the screw-height of the spiral is so small and the filaments moreover have the

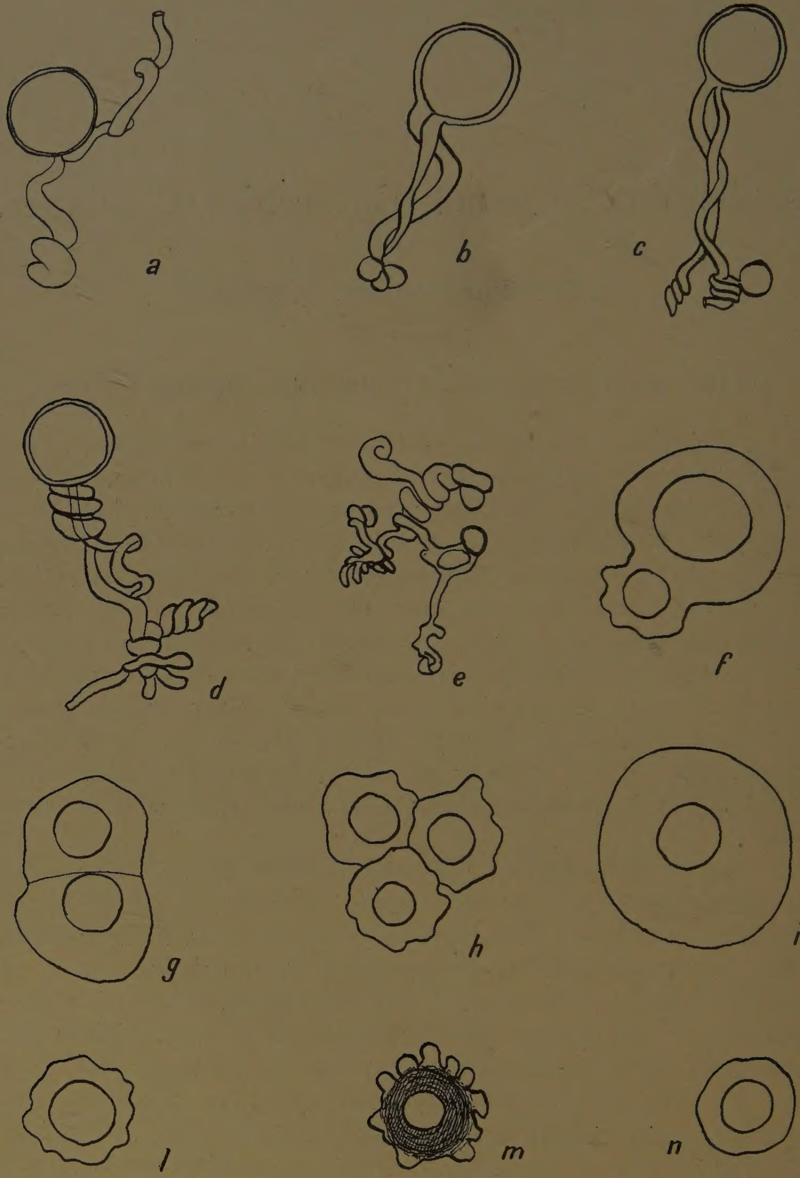

Fig. 1. *E. digitata* LAGERH. *a*—*e*: Spore formation, cfr. texte, figured from material communicated by prof. LAGERHEIM. *f*—*n*: Various forms of spores and spore complexes, figured from material, collected by Nordby on Fanø, see pg. 7. *a*—*e*: about $\frac{1300}{1}$; *f*—*n*: $\frac{600}{1}$.

plasm so dense and refractive that it is almost impossible to decide, whether a single or two filaments take part in forming the spiral.

From our observations we are justified in concluding the following: The spore originates from two spiral filaments fusing together, which at least in many cases are twined around each other, while in other cases it is probable that they fuse without twining. The spiral threads themselves are coming from very complex hyphal bundles and may often be branched (fig. 1, *d—e*). Sometimes two spores are formed connected to each other, so the double-spore strikingly is resembling a teleutospore of a *Puccinia* (fig. 1, *g*). In other cases three spores are growing together forming a row or a *Triphragmium*-like complex (fig. 1, *h*), and also four spores are observed in connection. Rarely one of the two spores forming a »Puccinia« has a smooth membrane, while the other one is coarsely warted (fig. 1, *f*). In no case we have happened to see a spore with only one adherent spiral string; this circumstance naturally by no means excludes the possibility of the spore being formed by a single filament, but at least it is the rule that two spiral filaments directly take part in the spore formation, a phenomenon, which reminds of the ascus formation in the genus *Eremascus*.

II. The systematic position of the genus Entorrhiza.

The genus *Entorrhiza* has always been considered by the authors as a relative to the Ustilagineae, until BREFELD (1912, p. 80) brings forward the opinion that the fungus probably must be regarded as a *fungus imperfectus* belonging to the Ascomycetes, the ascus-form of which is still unknown. In the said paper BREFELD has proved indisputably that an »*Ustilago*« on *Panicum crus ardeae* WILLD.[1]) from South America really is a conidial stage of a *Claviceps*-like Hypocreacea, viz. *Ustilaginoidea* BREF., the existence of which he already several years ago had profezied. Further he is probably justified in his conclusion that the morphologically thoroughly like *Ustilago virens* CKE. (= *Tilletia Oryzae* PAT.) on rice belongs to the same genus. BREFELD, however, is going still farther in so far as he, as it appears less convincing, also classifies the genera *Entorrhiza* WEBER and *Schroeteria* WINT. as *fungi imperfecti* among the Ascomycetes. He is led to this

[1]) By BREFELD »*Panicum crus Urdeae*«, probably erroneous for the said species.

supposition mainly by studying the manner of spore germination. He has namely found in both genera that the spores are germinating into short flash-shaped sterigmata on the top of which are formed basipetal chains of conidia, a fact stated for *Schroeteria* long ago, but until then not observed in *Entorrhiza.* This manner of germination into »*Acrostalagmus*-like« conidia, which was observed by Brefeld in the species *Entorrhiza Aschersoniana* (Magn.) De Toni, *E. cypericola* (Magn.) De Toni, *Schroeteria Delastrina* (Tul.) Wint. and *S. parvispora* Bref. might point, undeniably, towards a relationship to the Ascomycetes, but Brefeld seems not to take in consideration nor at least to lay stress upon the fact that previous investigators have observed that the spores of the genera in question can germinate in an ustilaginoid manner. Thus Winter (l. c. p. 147) has found that *Schroeteria Delastrina* may germinate into a *Tilletia*-like promycelium, and Weber states l. c. that the germination of *Entorrhiza Aschersoniana* is going on in that way that the spore sends out several hypha-like promycelia which again produce falcate sporidia, as well laterally as apically, thus putting in mind the germination of a *Proustilago.* These facts point clearly towards a relationship to the Ustilagineae, and so it may be reasonable to believe that the germination into »*Acrostalagmus*-like« conidia is a phenomenon of secondary importance.

In fact, the morphological likeness between the genera *Entorrhiza* and *Schroeteria* and, on the other side, the conidial stage of *Ustilaginoidea*, is not very great: The greenish *Sepedonium*-like chlamydospores of the last fungus are formed on the surface of a solid central pseudoparenchyma, which in some cases can appear as a real sclerotium, a circumstance, which in connection with the occurrence of the fungus in the ovaries of grasses, puts in mind a *Claviceps*-like organism — while on the other hand *Schroeteria* and *Entorrhiza*, owing to their perishable hyphae and the formation of entirely dust-like spore-masses, resemble the true Ustilagineae.

As to the genus *Entorrhiza* the spore-formation in *E. digitata*, described above, furthermore seems to be like that of the Ustilagineae in several respects. In this group cell-fusions by deliquescence of the membranes are commonly occurring during the spore formation, and recently F. Rawitscher has shown that the young binucleate spore cell in *Ustilago Maydis* results from the dissolving of a wall between two uninucleate neighbour-cells. Further the intricately entangled hyphal complexes, wherefrom the sporogene

hyphae originate in *Entorrhiza digitata*, have a striking likeness with the corresponding organs in the true Ustilagineae, not least by the marked deliquescence of the filaments (fig. 1, *e*).

Concerning the cytology of the Ustilagineae Dangeard, Lutman and Rawitscher l. c. have shown that a syncaryon-stage is established earlier or later during the ontogenesis, the young spores obtaining always two nuclei which later on fuse together

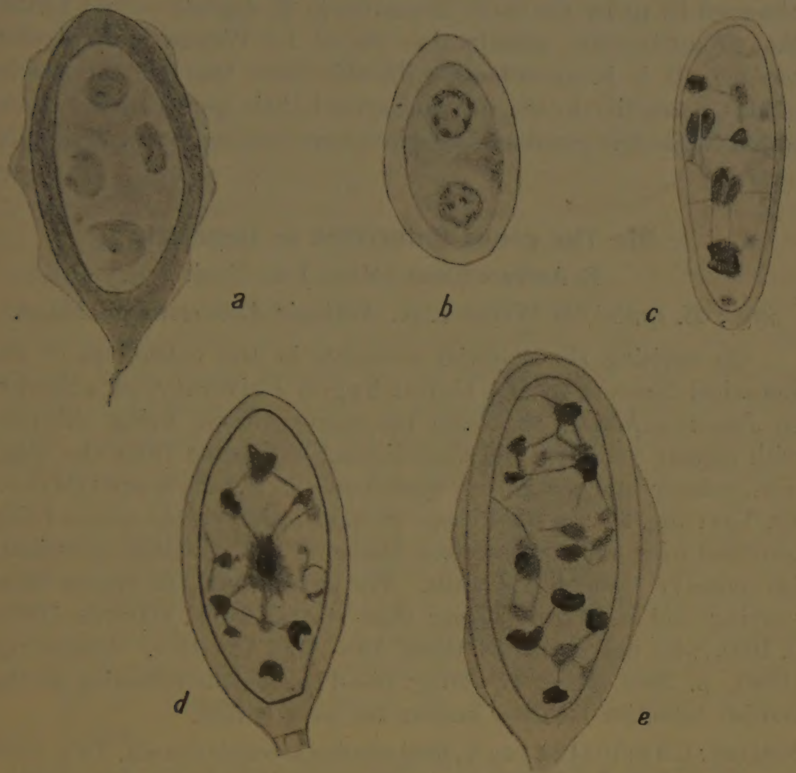

Fig. 2. *E. Raunkiæriana* sp. n. *a—b*: Spores with few rather distinct nuclei. *c—e*: Spores with numerous chromatin bodies in the cytoplasm. $\frac{2400}{1}$.

within the spore. — As to *Entorrhiza* we have not succeeded in making out its cytology, but in several cases we have seen that the spores as well in *E. Raunkiæriana* sp. n. (fig. 2, *b*) as in *E. digitata* have two rather distinct nuclei. Often, however, the nuclear elements have another appearence. Thus, in *E. Raunkiæriana*, three or more nucleus-like organs (fig. 2, *a*) are to be seen in the cytoplasma, but mostly distinct nuclei are not present, a number of chromatin bodies being scattered all around in the

plasm, without nuclear membrane, and connected to each other with linin threads (fig. 2, *c—e*)[1]).

In conclusion it seems to be justified — in spite of the »*Acrostalagmus*-like« germination — to place *Entorrhiza* and probably also *Schroeteria* in the neighbourhood of the Ustilagineae. Especially *Entorrhiza* might be considered as a primitive type of the said group on account of the morphologically well marked copulation observed by us by the spore formation in *E. digitata* — and further the *Proustilago*-like germination stated by Weber in *E. Aschersoniana.* It is in accordance with this view that all the species of this genus live in the soil and spread their spores by aid of the water, while the genuine Ustilagineae are adapted to an aërial life.

III. The genus Entorrhiza in Denmark.

E. Aschersoniana (Magn.) de Toni.

Syn.: *E. cypericola* Weber e. p., *Schinzia Aschersoniana* Magn.

On revising the material available in the collections of the Botanical Museum of the Copenhagen University, all collected on *Juncus bufonius*, we found the spores always being elliptical with regular sculpture and thus distinctly differing from the spherical, coarsely and unregularly warted ones in *E. Casparyana* (Magn.) De Toni (fig. 8). In some cases we have observed the spores being provided with adherent screwed filaments and channels (germination pores?) through the walls. We have found the spores more varying and as a rule bigger than stated by P. Magnus (1888, p. 103), who has measured them $15—17 \asymp 11—15\,\mu$. Schroeter (1889, p. 290) states $17—20 \asymp 15—17\,\mu$. In the following all the Danish localities hitherto known are enumerated.

Sealand: Charlottenlund, field sloping towards the sea. July, 1885 (E. Rostrup). Spores yet immature. A single one $17^1/_2 \asymp 15\,\mu$.
Constantia, Aug. 14, 1885 (E. Rostrup). Sp. $16—22 \asymp 12—18\,\mu$.
Rørvig, June 21, 1914 (C. Ferdinandsen). Sp. immature, $17^1/_2 \asymp 15\,\mu$.

Jutland: Randbøldal, Sept. 12, 1885 (E. Rostrup). The material destroyed. A single spore $20 \asymp 15\,\mu$.

[1]) In this connection we can state that in *Schroeteria Decaisneana* (Boud.) De Toni we have seen as a rule two nuclei in the young spores, a single or three though being also observed (c. 60% : 2 nuclei, c. 30% : 1 nucleus, c. 10% : 3 nuclei).

Treldeskov, July 9, 1886 (E. ROSTRUP). Spores 19—24 ⋍ 16—21 μ.

Klitmøller, July 1894 (E. ROSTRUP). The more coarsely warted spores 20—22 ⋍ 17½—19 μ.

Further LIND (l. c. p. 271) reports: Sæby (E. ROSTRUP) and Frederikshavn (LIND).

Bornholm: LIND (l. c. p. 271) reports: Almindingen (E. ROSTRUP).

E. digitata Lagerh.

To this species must be referred three numbers, all collected by dr. C. H. OSTENFELD on the western coast of Jutland. The two numbers (Fanø and Tværsted) were found on a plant of the *Juncus articulatus*-group, which dr. OSTENFELD believes to be a distinct form of *Juncus alpinus* Vill. He has friendly communicated to us that the infected specimens of this *Juncus* on the Fanø-locality grew mixed together with plants of *J. atricapillus* Drej. and *J. lamprocarpus* Ehrh. without these two species being found infested by the fungus. The third specimen of this *Entorrhiza* was found on a seedling of a *Juncus articulatus* s. lat. impossible of a closer determination; on the locality (the lake Ferringsø near Bovbjerg) the *Juncus alpinus*-form in question may very well occur, and it is thus probable that we also here are dealing with this plant. LAGERHEIM l. c. gives as host-plant *J. articulatus*. Judging from the localities (Titisee Germaniae, Pontresina Helvetiae) it is probable that under this collective species-name is hidden a *Juncus alpinus*-form, the *Entorrhiza*-species showing to be very specialized to single species of host-plants.

In the following are given the localites and some details of the fungus.

Jutland: Ferringsø, July 1893. On a seedling of »*Juncus articulatus*« (C. H. OSTENFELD). LIND (l. c. p. 271) reports this specimen as *Entorrhiza Aschersoniana* on *Juncus bufonius* in accordance with a label written by the late prof. E. ROSTRUP. Spores as described in the specimens from Fanø, 17½—22 μ diam.

Tværsted, strand dune, Aug. 10, 1912. On *Juncus alpinus* Vill. forma (C. H. OSTENFELD). Exactly agreeing with the following.

Fanø, near Nordby, Oct. 15, 1912. On *Juncus alpinus* Vill. forma (C. H. OSTENFELD).

In the specimens from the last named locality the tumours were found to be now cylindrical, entire, now more or less palmate. Spores spherical, pale yellowish-chestnut according to the advancing maturity, as a rule 20 μ across, many lesser, some bigger, some others gigantic, until 45 μ across, the wall then being exceedingly thickened (fig. 1, *i*). The shape of the membrane is very varying. In some cases the membrane is entirely smooth and then commonly being very thickened, often about 10 μ, surpassing the diameter of the lumen. The membrane of the above mentioned gigant-like spore was about 18 μ thick. In other cases the spores are provided with very long (about 5 μ), obtuse or flattened warts being irregularly distributed on the surface of the membrane, putting in mind the sculpture of the *E. Casparyana*-spore (fig. 1, *m* and fig. 8). Finally some spores are more regularly and lower warted (fig. 1, *l*). On studying more thoroughly the material, one often finds two or more spores connected with each other in a *Puccinia*- or *Triphragmium*-like complex (fig. 1, *f*—*h*) or seldom in a row composed of some few spores. Often we have seen channels going through the thickened walls.

Entorrhiza Raunkiæriana Ferd. et Wge. sp. n.

Mycocecidiis ex apicibus radicum tenuium tumefactis oriundis, oblongo-citriformibus vel ovoideis, formam siliquae *Crambes maritimae* L. saepe aemulantibus, maximis 3 mm latis, albo-flavidis. Sporis in hyphis hyalinis, diu persistentibus acrogenis, ± protracte ellipsoideis, citriformibus, plerumque 18—21 μ long. ≍ 9—11 μ lat., nonnullis usque ad 30 μ elongatis, hyalino-flavidulis, plasmate denso, nonnumquam vacuolato farctis, episporio lineolis spiralibus, circ. 2 μ inter se distantibus, dextrorsum oblique ascendentibus ornato suffultis.

In radicibus *Scirpi fluitantis* L., in stagno dunensi Grøndal dicto insulae Danicae Fanø submersi, mense Octobri. (Leg. C. Raunkiær).

This fungus, which by J. Lind (l. c. p. 271) is identified with *E. scirpicola* (Correns) Sacc. et Syd., was already found in the year 1896 by prof. C. Raunkiær in a little dune-lake, Grøndal, on the island of Fanø, and was refound Septbr. 1911 and Oct. 1912 in the same locality. A great many roots of *Scirpus fluitans* submerged outside the *Agrostis canina*-community were infested by the fungus. — Spores collected in Oct. were wintered at a low room temperature, apparently without changing their aspect. As

late as March 10 the curved appendix persisted in nearly all the spores, and no germination was to be seen.

As to be exspected the species has a considerable resemblance to *E. scirpicola* on *Scirpus pauciflorus* Lightf., but differs distinctly from this as well by the shape of the tumours as by the spore-form. In *E. scirpicola* the tumours are cylindrical (fig. 5) while in our species ovoid or often constricted as the silique of *Crambe maritima* L. (fig. 3). Further the spores in *E. scirpicola* are less slender (16—20 ⋍ 11—14 μ) than in *E. Raunkiæriana* (18—21 ⋍ 9—11 μ), the proportion between length and breadth of the spores in the two species thus being respectively 1,5 : 1 and 1,9 : 1 (fig. 4 and 5). We have not succeeded in procuring type-specimens of *E. scirpicola*, but still we have had occasion to examine this species; in the collections of the Botanical Museum of the Copenhagen University are found, namely, specimens of the fungus on *Scirpus pauciflorus* from the Færøes (Trangisvaag on Suderø, leg. C. H. Ostenfeld); E. Rostrup (1901, p. 306) identified the plant with *E. cypericola* (Magn.) De Toni. In these specimens, though being very young, so that the spiral lines of the spore-membrane just are going to appear, the proportion between length and breadth of the spores still is exactly as stated by Correns, the young spores measuring 15 ⋍ 9 μ.

Fig. 3. *E. Raunkiæriana* sp. n. Tumours in roots of *Scirpus fluitans* L. About nat. size.

Fig. 4. *E. Raunkiæriana* sp. n. Spores, one of which showing in optical section the outer structure of the membrane, and another showing the same structure in transverse section. Cfr. fig. 2. $\frac{700}{1}$.

Fig. 5. *E. scirpicola*, (Correns) Sacc. & Syd. *1—3*: Rootswellings on *Scirpus pauciflorus* Lightf.; *4—5*: Spores from above and from the side; *6*: Spore from above, treated with conc. H_2SO_4. *1—3*: $^1/_1$; *4—6*: $\frac{500}{1}$. After C. Correns.

The record of this fungus from the Færøes, being so far away from the hitherto only known locality, Val Maggia, Tessin, Switzerland, suggests the opinion that the distribution of the *Entorrhiza*-species is coincident with that of their host-plants and that the species are closely specialized to single

host-species. In this connection the above statement under *E. digitata* might be brought to memory, and further that the hitherto known *Entorrhiza*-species, which seem to be distinctly different, every one is confined to a single host-species.

The two species of *Entorrhiza* growing on *Scirpus* are both characteristic by having spiral lines on the spore-membrane, in this regard differing from the other species of the genus. As stated above they are, however, morphologically well separated, a circumstance, which was likely to be found, partly because the *Entor-*

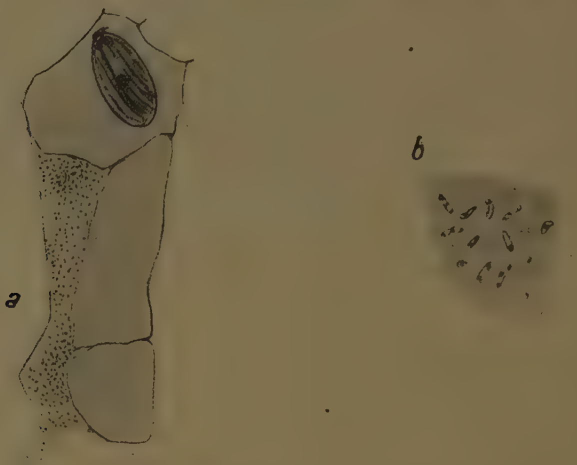

Fig. 6. *a*: Bark cells from a root of *Scirpus fluitans* L., infested by *E. Raunkiæriana* sp. n. In one cell is seen a spore of the named fungus, in another numerous bacteria. $\frac{700}{1}$. *b*: The bacteria higher magnified. These bacteria were commonly found in our material.

rhiza-species upon the whole are strongly specialized to their host-plants, and mainly according to the fact that the host-species in question belong to different subgenera, *S. pauciflorus* being an *Euscirpus*, while *S. fluitans* belongs to *Isolepis* and even by Link is referred to a particular genus, *Eleogiton.*

Entorrhiza caricicola Ferd. et Wge. sp. n.

Aggressu fungi, qui apices radicum tenuium infestat, tumoribus piriformibus vel oblongo-piriformibus, levibus, maximis 3—4 mm. longis et 1—2 mm. latis, albidis oriundis. Sporis in hyphis hyalinis, deliquescentibus, plerumque tortis acrogenis; episporio primum levi, hyalino, indumento gelatinoso instructo, ad maturitatem, contractione strati gelatinosi, subtiliter ruguloso-undulato, dilute flavidulo. Sporis maturis oblongo-ellipsoideis vel protracte obo-

voideis, saepius inaequilateralibus, ad insertionem stipitis applanatis, 22—26 μ long. ≍ 12—16 μ lat., plasmate denso, vacuolato farctis.

In radicibus tumefactis *Caricis limosae* L. in palude Lyngby Mose dicta Selandiae septentrionalis, mense Septembri. (Leg. F. Kølpin Ravn).

Fig. 7. *E. caricicola* sp. n. Spores $\frac{600}{1}$.

E. Rostrup (1894, p. 36) mentions this discovery and identifies the specimens collected with *E. cypericola* (Magn.) De Toni parasiting in the roots of *Cyperus flavescens* L. Yet he adds: »The form found on the said *Carex* differs, however, as to the size and structure of the spores somewhat from the description given by P. Magnus, it therefore possibly being a distinct species, which must be verified by direct comparison and culture experiments. The spores are somewhat larger than those of Magnus, being namely 20—25 ≍ 12—15 μ«.

In fact, the morphological difference between the two species is rather great, as well regarding the shape of the spore as the sculpture of the membrane, which has been evident to us by examining specimens of *E. cypericola* from the classic locality. We found the size of the spores agreeing with the statement of P. Magnus (17—20 ≍ 11—14 μ), wherefrom it thus becomes evident that the spore in *E. cypericola* is relatively considerably broader than in *E. caricicola*, the proportions between length and breadth being respectively 1,4 : 1 and 1,7 : 1 (fig. 7—8). Further the membrane in *E. cypericola* is thicker and more coarsely sculptured than in our species. We can state that by examining *E. cypericola* we often have found the spores provided with two adherent filaments, and that we also in this

Fig. 8. Spores of: *1—2*: *E. cypericola* (Magn.) De Toni; *3—4*: *E. Aschersoniana* (Magn.) De Toni; *5—6*: *E. Casparyana* (Magn.) De Toni. c. $\frac{650}{1}$. (After P. Magnus).

species have observed two spores connected into *Puccinia*-like complexes.

Entorrhiza caricicola sp. n. which is the only *Entorrhiza*-species known on the genus *Carex*, is found on *Carex limosa* L. in a bog near Lyngby in the northern Sealand, first by prof. F. Kølpin Ravn in Septbr. 1893, later by dr. C. H. Ostenfeld »in radicibus *Caricis limosae* inter muscos; Selandiae, Lyngby, in turfosis. 27. 10. 1895«.

By J. Lind (l. c. p. 271) the fungus is enumerated under the name adopted by E. Rostrup: *E. cypericola* (Magn.) De Toni.

IV. The species of the genus Entorrhiza.

The genus *Entorrhiza* was founded by C. Weber in 1884 (l. c) upon the *Juncus bufonius-Entorrhiza*, *E. Aschersoniana* (Magn.) De Toni, which thus must be considered as the type species. It is the merit of P. Magnus, however, to have signalized to science the first species of this genus in that he already in 1878 published his *Schinzia cypericola* (1878, p. 53); this mycologist namely was of opinion that his fungus belonged to the genus *Schinzia* founded by K. Nägeli in 1842 (l. c., p. 281) on *Schinzia cellulicola* in the roots of *Iris* sp.

Whatewer it may be one must maintain that the belonging together of the two last named species is very doubtful, because Nägeli in his description and figures of *E. cellulicola* omits some features exceedingly characteristic of the genus *Entorrhiza*. Further the integrity of the genus *Schinzia* has been shaken by authors who have referred quite heterogeneous elements, viz. *Schinzia Alni* Wor. and *S. Leguminosarum* Frank, to this genus.

The point of view being justified that *Schinzia cellulicola* Näg. is not a true *Entorrhiza* and considering furthermore the *E. Solani* Fautrey (l. c.) as problematic, the genus *Entorrhiza* thus shows to be confined only to glumiflorous host-plants, even if the tumours of the plants mentioned by P. Magnus (1888, p. 104) might turn out to be produced by fungi belonging to this genus.

In conclusion the following organisms must be considered as true *Entorrhiza*-species:

On *Juncaceae*:

E. Aschersoniana (Magn.) De Toni (*Juncus bufonius* L.).
E. Casparyana (Magn.) De Toni (*Juncus Tenageja* Ehrh.).
E. digitata Lagerh. (*Juncus articulatus* L. coll., probably always *J. alpinus* Vill.).

Further C. B. Plowright (l. c., p. 299) and E. Rostrup (1901 p. 306) state the presence of an *Entorrhiza* in the roots of *J. lamprocarpus* Ehrh.

On *Cyperaceae*:

E. cypericola (Magn.) De Toni (*Cyperus flavescens* L.).
E. scirpicola (Correns) Sacc. et Syd. (*Scirpus pauciflorus* Lightf.).
E. Raunkiæriana sp. n. (*Scirpus fluitans* L.).
E. caricicola sp. n. (*Carex limosa* L.).

Probably several other glumiflores will show to be host-plants to *Entorrhiza*-species — e. g. the plants with root-swellings enumerated by P. Magnus (1888, p. 104) after a statement of P. Cameron, viz.: *Juncus squarrosus* L., *J. uliginosus* Roth and *Eriophorum vaginatum* L.

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